THE LARVAL DEVELOPMENT OF THE CALIFORNIA SPINY LOBSTER, *PANULIRIS INTERRUPTUS* (RANDALL), WITH NOTES ON *PANULIRUS GRACILIS* STREETS[1]

BY

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INTRODUCTION

The California spiny lobster, *Panulirus interruptus* (Randall), is the only lobster occurring on the coast of California. Its main distributional range is usually considered to be from slightly north of Point Conception, California, to the Gulf of Tehuantepec, Mexico.

For many years it has been a highly prized item in the fisheries of California and is considered eleventh in importance by value among the fisheries of the state (Wilson, 1948). The amount of research accorded the lobster has, however, not been commensurate with this economic importance or with its biological interest.

During its life history, the spiny lobster passes through a series of eleven floating larval "phyllosoma" stages in which the body is highly transparent and exceedingly compressed dorsoventrally. The last phyllosoma stage metamorphoses to a "puerulus" stage in which the animal is still transparent but structurally similar to the adult. The puerulus of some species may be found in plankton, but evidently it soon deposits calcium in the carapace and seeks the bottom to live in concealment.

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Allen (1916) carried out certain fundamental observations on the adult animals particularly in the vicinity of Santa Barbara, the Channel Islands, and La Jolla. His findings are especially pertinent to the present study in showing that the berried females may carry 5,000 to 500,000 eggs each, depending upon size, and that the spawning season extends from March to August with its maximum activity in May, June, and July. He concluded that a period of from nine to ten weeks is probably required for hatching. The young hatched readily in aquaria, but attempts at rearing
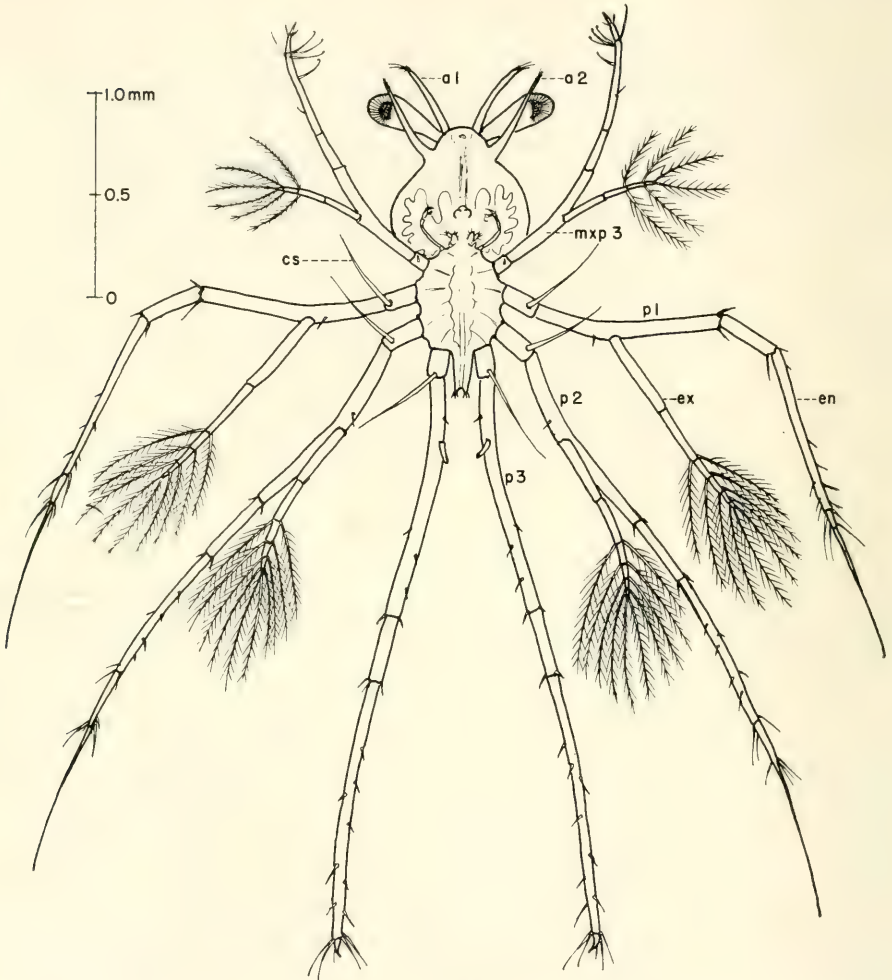
Figure 1. Stage I of *Panulirus interruptus* phyllosoma hatched in aquarium. Labels: *a 1*, first antenna; *a 2*, second antenna; *cs*, coxal spine; *en*, endopod; *ex*, exopod; *mxp 3*, third maxilliped; *p 1, p 2, p 3*, first, second, and third legs.

the larvae were futile. Other investigators have had similar experiences in attempts at rearing the phyllosoma larvae of other species. In a recent study, Lindberg (1955) found a maximum of 800,000 eggs produced by large females. The spawning season was essentially the same as indicated by Allen (1916).

With regard to our knowledge of the biology of phyllosoma larvae in nature, rather little is known because of their scarcity, coupled with the lack of complete and identified developmental series. Their offshore or oceanic distribution also adds to the difficulty.

In 1919 Schmitt published a brief note on phyllosoma larvae caught off the coast of southern California. Larvae of several sizes were observed. The details of structure and stages of development were, however, not worked out in any case, but a photograph was included showing a large specimen which appears to represent either the tenth or the eleventh phyllosoma stage.

A practical understanding of the biology of the California spiny lobster will require information regarding the abundance and extent of dispersal of its planktonic larvae from various areas within the geographical range of the species. It is probable that many of the larvae produced in the northern range of adult distribution are lost by drifting away from the area with the California Current. Unless many of the northern larvae are returned by some circuitous route in large local eddies, the maintenance of the local stock would depend in considerable measure upon recruitment of larvae from more southern waters, probably with the Davidson Current. A knowledge of the duration of the planktonic larval stages and the rate and direction of ocean currents is highly important in this connection, but we have no direct information on how long the larvae live in the plankton, though studies now in progress of the seasonal distribution of the stages point to a planktonic period of several months.

The series of phyllosomas examined from plankton collections along the California coast to south of Cedros Island have not revealed any significant irregularity in structure, shape, or size, of the various developmental stages, indicating that only one species is involved in the northern range. However, *Panulirus gracilis* (until recently known as *Panulirus inflatus* (Bouvier)) does overlap the southern range of *Panulirus interruptus* at least in small numbers and enters into the commercial catch of Mexico (Chase and Dumont, 1949). In a review of the conflicting synonymy of *P. inflatus*, Holthuis (1954) has concluded that the species is a synonym of *P. gracilis* Streets. The latter, being the older name, must be used.

The larvae of *P. gracilis* may be expected to drift northward should they be caught in the Davidson Current, especially during its maximum development along the coast. For this reason, among others, it is essential

that the larval structure be known in detail in order to facilitate definite identification of the planktonic stages of the two species. This identification can now be made as a result of a study of larvae caught within the range of *P. gracilis* south of Point Eugenia and within the Gulf of California. The larvae of the two species are distinguishable on small but definite structural characteristics, which will be briefly mentioned here and reported upon in detail later.

A survey of the seasonal and spatial distribution of the larvae is in progress.

The Phyllosoma Stages of P. interruptus

Large numbers of the first phyllosoma stage were obtained in 1940 by hatching of eggs from a berried female kept in an aquarium (figure 1). Subsequent stages (figures 2 to 18) were all obtained from plankton hauls, especially from collections made along the coasts of southern and Baja California in connection with the Marine Life Research Program of the California Cooperative Oceanic Fisheries Investigations.

Careful anatomical analysis of large numbers of larvae reveals eleven rather poorly defined developmental stages as summarized in table I. There is a considerable range in size within each "stage," especially in the later stages, and specimens are often observed in which structures such as newly added legs, exopods, gills, second maxillae, and first maxillipeds show noticeable range in size or shape or even degree of segmentation. Whether or not this signifies a molt within the stage is not known, but it may be significant that the more advanced occur in the upper-size range for the stage represented.

The fore-body (cephalic shield) of *Panulirus interruptus* is pear-shaped in outline in the early stages, and is much wider than the hind-body (thorax) during the first and second stages. But in the third stage, the hind-body has attained the width of the fore-body and remains thus during the subsequent stages. The pear-shaped fore-body of the earlier stages later becomes more uniformly oval as shown in figure 18. In no stage is the posterior margin of the hind-body deeply indented.

In stage I, the eyes are not stalked, but in stages II to XI, they are on definite slender stalks which increase steadily in length with each molt. In all stages there is present a median eye spot.

The *first antennae* (antennules) exceed in length the *second antennae* (antennae) during the first four stages, after which the second antennae

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Figures 2–5. Stages of *Panulirus interruptus* phyllosoma (continued). Labels: *p 3, p 4*, third and fourth legs. The distal ends of lengthy appendages showing no significant changes from stage to stage have been omitted in these and subsequent figures.
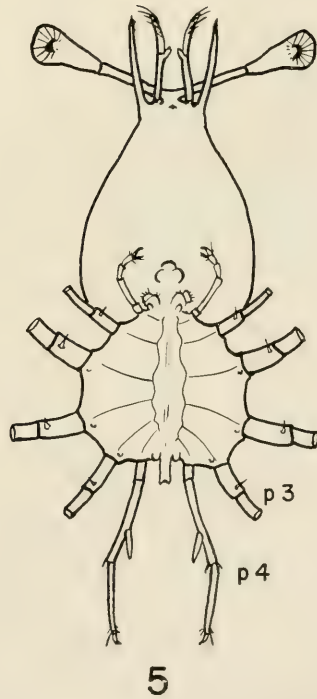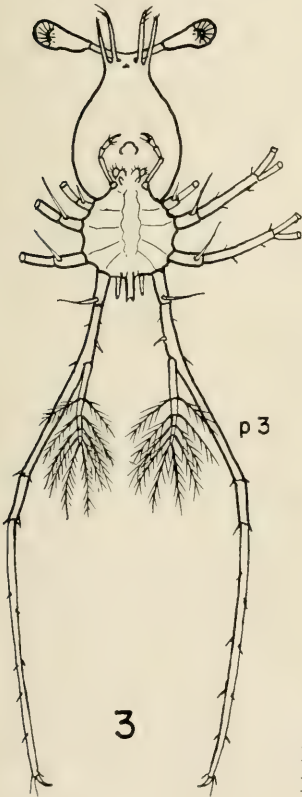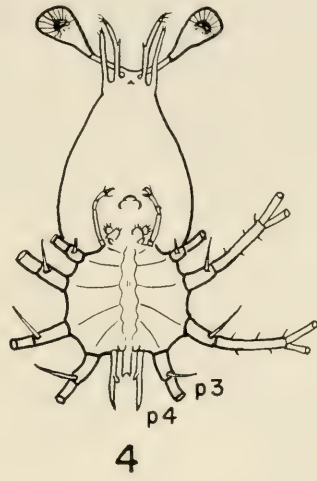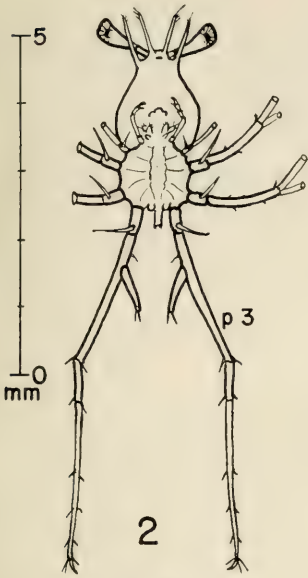
Figure 2.   Stage II.
Figure 3.   Stage III.
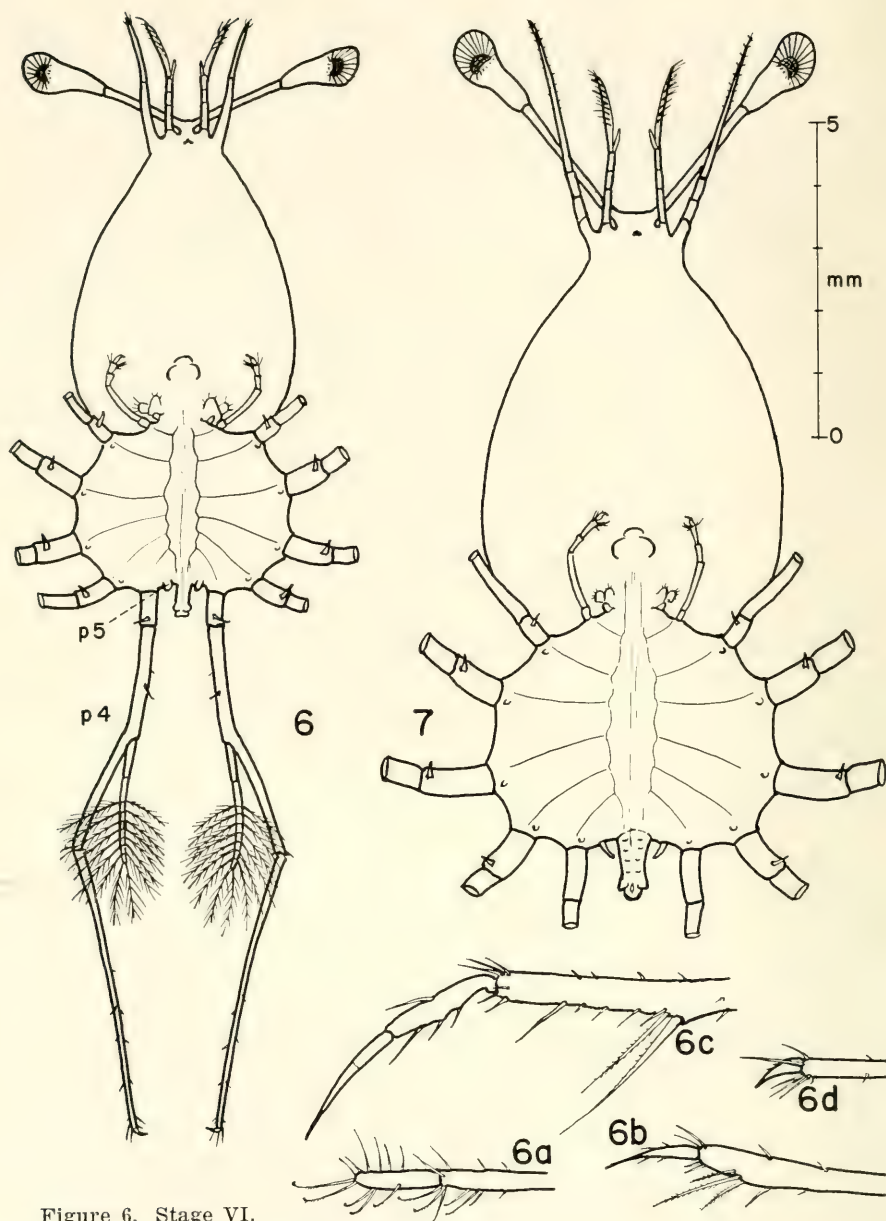Figure 4.   Stage IV.
Figure 5.   Stage V.

Figure 6. Stage VI.
Figure 6a. Stage VI, Tip of third maxilliped.
Figure 6b. Stage VI, Tip of first leg.
Figure 6c. Stage VI, Tip of third leg.

Figure 7. Stage VII.

Figures 6–7. Stages of *Panulirus interruptus* phyllosoma (continued). Labels: *p 4*, *p 5*, fourth and fifth legs.

progress rapidly with each successive stage until in stage XI they exceed in length the fore- and hind-body combined.

In stage I, the distal end of the first antenna bears a tuft of 4 setae and in each subsequent stage additional tufts are added proximally as transverse rows of setae. The endopod is first evident as a low bud in stage IV. In following stages it elongates, becoming a true branch, but remains small throughout the development and is not a free segment until stage VIII. Beginning in stage VI (sometimes stage VII), there are three segments in the peduncle, the first segment being equal to the combined lengths of segments two and three which are subequal. These proportions remain about the same in the next two stages, but in stages VIII–XI the third segment is somewhat longer than the second though both combined still equal the length of the first segment.

The second antennal peduncle becomes three segmented in the seventh or eighth stage. These segments remain about equal, the third being slightly the longest.

The structure of the *mandibles* and the first *maxillae* in stage XI is shown in figure 16. These appendages are very short and strong. The mandibular blade, when viewed from the ventral side of the larva, is seen from the edge. In figure 16, it is tilted slightly and the labrum lifted to show the broad scoop-shaped blade with the stronger teeth at the outer and inner angles. The two branches of the first maxillae are armed respectively with three strong hooks and three flexible setae, but prior to stages VII and VIII there are only two hooks and setae. There is present a small vestigial palp bearing two setae. In stage I the palp is prominent but diminishes in intermediate stages and later again enlarges.

Thus these mouthparts, together with the second maxillipeds which are armed at the tips with small claws and heavy setae (figure 15) indicate that the larva must feed upon particulate material gathered without the aid of a real filtering device.

The *second maxillae* in the first stage are composed of two segments, the distal one being much narrower. Each segment bears four long setae which in intermediate, and later stages are lost or shortened. There is but little change in this size relationship (figure 11) until about the sixth stage and in ensuing stages when the segments become noticeably flattened and the distal segment increases greatly in breadth especially posteriorly (figures 12–15). Similarly the first maxillipeds are at first simple buds which in the later stages gradually increase to three-lobed appendages (figure 15).

The *second maxillipeds* are functional feeding appendages in all stages. There is no change from the first until the eighth stage when an exopod bud appears. In stage IX, this bud becomes separated as a short segment which in the next stage elongates and bears 2 to 4 setae at the tip and

a gill bud appears on the distal portion of the coxa. In stage IX, the exopod has become setose with five or six pairs of setae, the gill has become leaf-like, and a second gill bud has appeared on the proximal portion of the coxa.

The *third maxillipeds* are very long and the exopod is already present and setose in the first stage. With each successive stage there is, however, an increase in the number of segments in the exopods. The number of segments as shown by the number of pairs of setae appears to be regular for each of the earlier stages, but become irregular in the later. The range in numbers of exopod segments for the third maxillipeds and the first and second legs for stages I to XI is respectively: 4 to 25; 6 to 32; and 6 to 33.

The principal features of the development of the legs, especially the third, fourth, and fifth pairs, are adequately covered in table I which, together with the figures, will show the changes taking place with each stage. In contrast to the rapid development of the fourth legs, the fifth pair remain as very small buds through stages III to VII, and never exceed the abdomen in length. In no stage of the development of the legs is there present a strong spine at the distal end of the second basipods as shown for *Panulirus gracilis* (figure 22).

The inner branches of the legs are readily lost so that a complete attached set of legs has not been found beyond the sixth stage, but judging from loose appendages found in the jar with the later stages the end segments do not change after stage VI (figures 6a–6d).

Coxal spines are present in the first to ninth stages, but are usually all lost in the tenth, and are never present in the eleventh.

In stage X *gills* are present on the dorsal distal end of the coxal segment of the maxillipeds and legs and in stage XI they occur also on the proximal portion of the coxa at the juncture of the carapace and on the dorsal margin of the thorax at the base of these thoracic appendages.

In stages V to XI, there are present spines on the ventral surface of the thorax at the bases of the third maxillipeds and each of the legs.

The *abdomen,* in stages I to V, remains about the same with two small points at the tip. Complete segmentation occurs in the ninth stage though earlier indications of segments may be seen as blocks of tissue under the skin.

The *uropods* become evident as buds in the sixth stage. They increase in size and definition with each successive stage and in stage IX are well-formed biramous appendages, but the rami are not separated from the basipods and their outer edges are entire. Upon reaching the tenth stage, the uropods are completely segmented and a small notch with a marginal

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Figures 8–17. Stages of *Panulirus interruptus* phyllosoma (continued). Labels: *ex,* exopod; *g,* gill; *mx 2,* second maxilla; *mxp 1, mxp 2,* first and second maxillipeds; *p 4, p 5,* fourth and fifth legs.
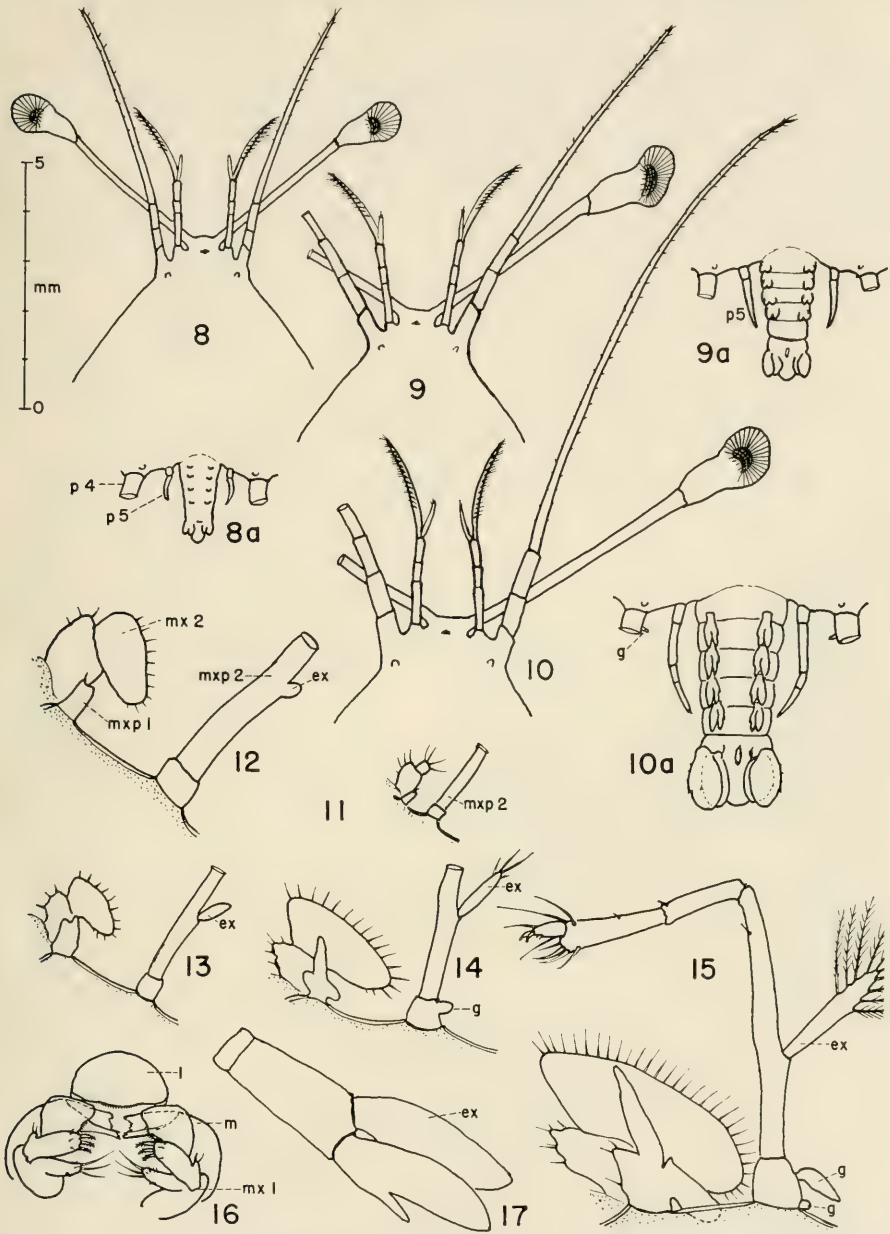
Figure 8.   Stage VIII, anterior end.
Figure 8a. Stage VIII, posterior end.
Figure 9.   Stage IX, anterior end.
Figure 9a. Stage IX, posterior end.
Figure 10. Stage X, anterior end.
Figure 10a. Stage X, posterior end.
(Figures 8–10a drawn to same scale.)

Figures 11–12. Stages IV and VIII, second
 maxilla with first and second maxillipeds.
Figure 13.   Stage IX, same, reduced scale.
Figure 14.   Stage X, same.
Figure 15.   Stage XI, same.
Figure 16.   Stage XI, mouth parts: labrum
 (l); mandible (m); first maxilla (mx 1).
Figure 17.   Stage XI, pleopod.

Table I
Panulirus interruptus—Phyllosoma stages
SUMMARY OF USEFUL DISTINGUISHING CHARACTERISTICS

Stage	length mm.	a 1	a 2	mxp 2	mxp 3	leg 1, 2	leg 3	leg 4	leg 5	pleopods	uropods
I	1.2– 1.5	1 seg.	1 seg.		ex. seto. cs.(small)	ex. seto. cs.	cs.	0	0	0	0
II	2.4– 2.8	1 seg.	1 seg.		same	same	cs. ex. 1 seg.	bud	0	0	0
III	3.3– 3.8	1 seg.	1 seg.		same	same	cs. ex. seto.	1 seg.	bud	0	0
IV	4.6– 5.2	1 seg. en. bud	1 seg.		same	same	same	1(2) seg. ex. bud	bud	0	0
V	6.0– 6.8	2 seg. en. bud	1 seg.		same	same	same	3 seg. ex. 1 seg.	bud	0	0
VI	7.9– 8.5	basis 2–3 seg. en. 1 seg.	2 seg. +		same	same	same	4 seg. ex. seto.	bud	0	low buds
VII	9.4–11.0	basis 3 seg. en. 1 seg.	4 seg. +		same	same	same	same	1 seg.	buds	buds (sometimes cleft)
VIII	12.9–16.0	same	same	ex. bud	same	same	same but no cs.	same	2(1) seg.	buds cleft	buds cleft
IX	16.0–19.5	same	same	ex. bud or 1 seg.	same	same	same	same	2 seg.	long buds cleft	biramous complete
X	19.0–24.3	same	same	ex. 1 seg. 1 g. bud	same 1 g. bud	same but no cs. 1 g. bud	same 1 g. bud	same 1 g. bud	4 seg.	unseg. biramous	same
XI	26 –31.2	same	same	ex. seto. 2 g.	same but no cs. 2 g.	same but 2 g.	same 2 g.	same 2 g.	4 seg. and claw	segmented biramous	same

a 1 = first antennae
a 2 = second antennae
cs = coxal spine present
en = endopod
ex = exopod

g = gill(s) on coxa
0 = wanting
s = segment (excluding claw)
seto. = setose
+ = longer than a 1

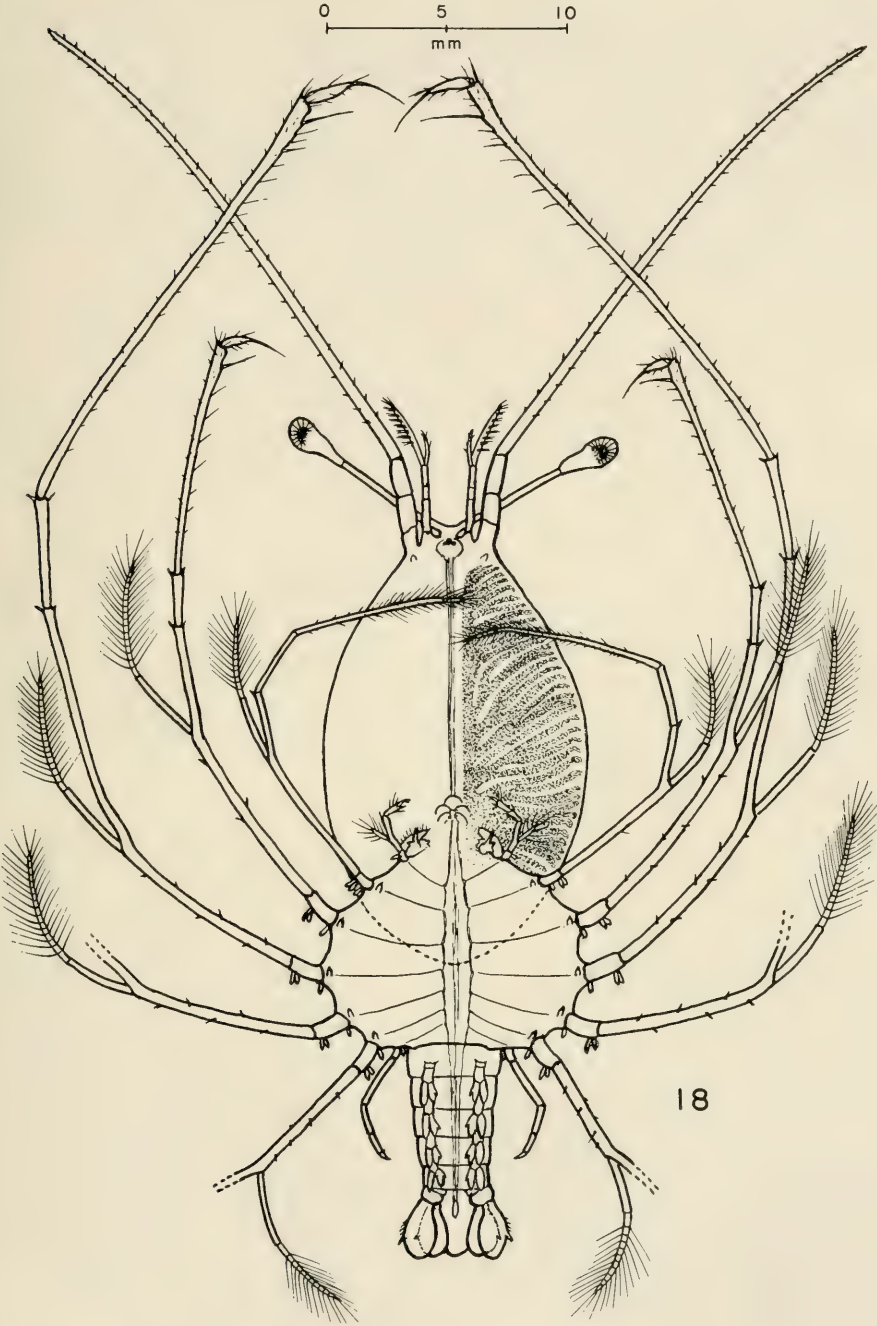See text and figures for further details.

Figure 18. Stage XI of *Panulirus interruptus* phyllosoma.

spine occurs on the outer margin of each branch (figure 10a). In the last stage, this notch and spine are more pronounced.

The *pleopods* appear first in the eighth stage, but they may be indicated earlier under the skin. In stage IX, they may appear either as blunt notched projections or somewhat more advanced, more elongated and flattened structures. In the next stage, they are more leaf-like and a notch appears on the inner margin of the endopod. Complete segmentation occurs in the last stage and the notch on the inner border now sets off a well-defined blunt spine-like process (figure 17).

THE PHYLLOSOMA OF PANULIRUS GRACILIS

Phyllosoma larvae of another species of *Panulirus* have been collected on 10 separate cruises at a total of 19 stations lying off Baja California, and on two cruises at eight stations in the Gulf of California. These larvae are being referred to *Panulirus gracilis,* the only other species known from the West Coast.

From figure 22, it will be seen that this larva resembles that of *Panulirus interruptus* but in distinction from that species, possesses a strong spine at the distal end of the basipod on the posterior dorsal side of the segment closely adjacent to the exopod of each of the first three pairs of legs (figure 22 sp.). The complete series of larvae have not yet been found, but the spine persists as a distinguishing characteristic up through at least the eighth stage. Other differences have also been observed, but more material is needed for further study.

THE PUERULUS STAGE OF PANULIRUS INTERRUPTUS

(Figures 19–21)

During the metamorphosis from the last phyllosoma stage to the puerulus, the cephalic shield of the phyllosoma is greatly reduced in length and width. The thoracic region is also narrowed and fuses with the cephalic shield to form the cephalothorax. Thus the two erstwhile leaf-like distinct anterior regions of the larvae now appear as one region (figure 19). This, however, remains to some degree dorsoventrally compressed and adult spination is beginning to appear on the dorsal surface. The abdomen has become slightly broader and noticeably longer. Other conspicuous changes include loss of the exopods of the thoracic appendages, reduction in the

Figure 19. Puerulus stage of *Panulirus interruptus*, dorsal view.
Figure 20. Puerulus of *P. interruptus*, diagrammatic habit sketch.
Figure 21. Puerulus of *P. interruptus*, first pleopods.

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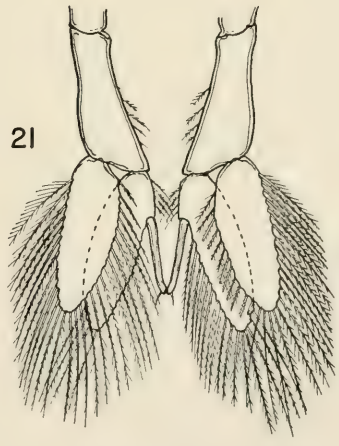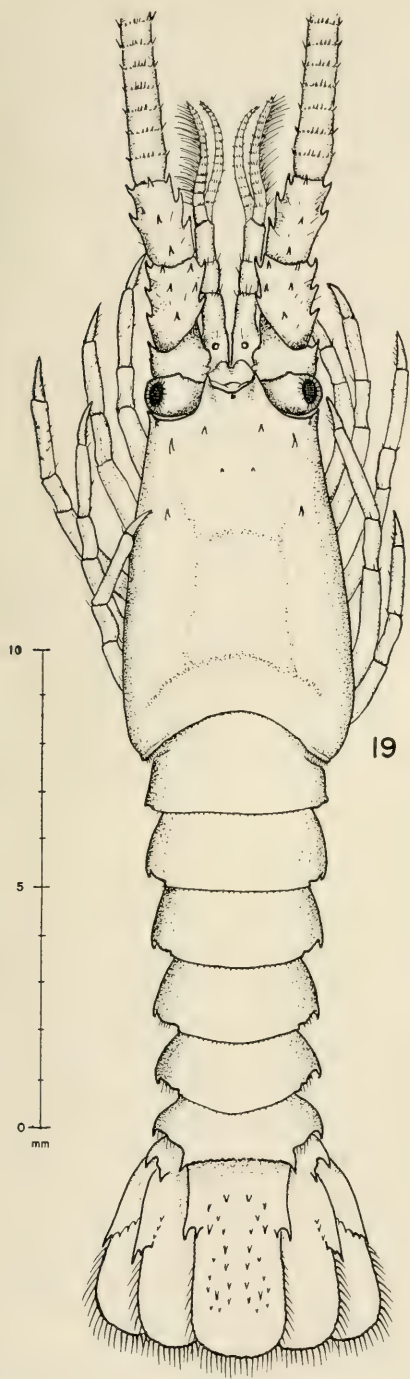
length of the eye stalks, and a greatly increased length of the second antennae to three times the body length.

The puerulus, while similar in appearance to the adult, is wholly transparent except for the eyes and pigment bands at intervals along the second antennae, and the walking legs are carried more laterally (figures 19 and 20). The larval median eye is still present and statocysts occur in the first segment of the first antennae.

The larval peripodal exopods which served as swimming organs in the phyllosoma stage are wanting and the animal is now apparently in the process of deserting the planktonic habit, but before deserting this pelagic existence the pleopods have developed into efficient swimming appendages. They have become heavily setose and each endopod bears a strong coupling process provided with hooks to interlock with a similar process of the opposite endopod (figure 21). Thus, in swimming, the appendages lend support to each other for more efficient propulsion.

Only a few specimens of the puerulus stage have been caught and these only from near-shore sampling at La Jolla, April, 1947; in Baja California at Bahia San Roque, September, 1949; and at Cedros Island, August, 1952, where John McGowan of Scripps Institution dip-netted four specimens. The animals are attracted to a light at night and most specimens have been caught in this way. The transverse dorsal grooves characteristic of the abdominal segments of *Panulirus interruptus* in older stages were not yet formed in the specimens. The size ranged from 20 to 21 mm. This agrees with the size reported by Gilchrist (1916) for *Jasus lalandii* in which phyllosoma of 33 to 35 mm. produced puerulus stages ranging from 22 to 26 mm. in length.

DISCUSSION

It has generally been assumed that the phyllosoma larvae are planktonic up to the puerulus stage. However, in experimental cultures Gilchrist (1916) found that after about six days the first phyllosoma larvae of *Jasus lalandii* avoid light and return to the bottom. But the evidence is not clear on this point for he mentions the possibility of larvae seeking the bottom following each molt. Von Bonde and Marchand (1935) make a similar statement regarding the first phyllosoma of that species, and Kinoshita (1934) indicates the same for *Panulirus japonicus*. In no case was the duration of the whole series of phyllosoma stages known.

Studies made on *Panulirus longipes* in Australian waters led Sheard (1949) to conclude that early phyllosomas are found in surface waters; the mid and late stages in mid to surface waters (migrating diurnally); and the late phyllosoma and puerulus stages in surface water. The duration of larval life was estimated to be about five months.

The phyllosoma larvae of the California spiny lobster have not been

taken in large numbers per haul in the plankton off the southern California coast. Usually they are widely dispersed and when present occur as one or a few individuals at a station. Stage I may, however, be quite abundant during August and September at coastal stations, especially off Baja California. The maximum concentration observed (cruise 28 station 105.32) was 488 per 1000 cubic meters of water strained by a 1-meter net. Data from analysis of plankton collected monthly over a period of several years from north of Point Conception to the tip of Baja California, and compris-
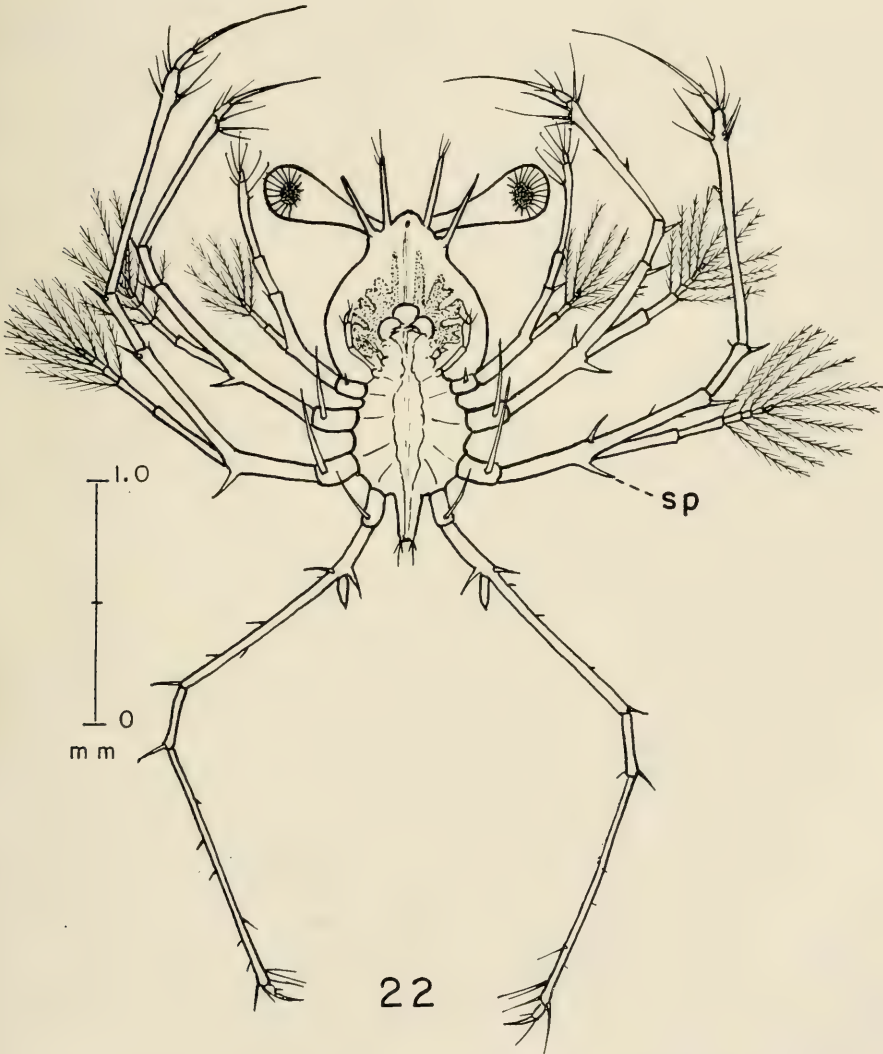

Figure 22. Stage I of *Panulirus gracilis* phyllosoma. Label: *sp*, spine.

ing hundreds of stations with routine sampling from 140–0 meters with a 1-meter net, show that complete cruises over the whole area sometimes yield no larvae whatever or only one to five late-stage individuals during January through May. More complete analysis of these data is needed and will be given in a later report. The finding of later stages floating above the 140-meter level in waters of depth ranging to several hundred meters and over 300 miles from shallow water shows that at least many of the larvae of our species do not seek the bottom regularly in the phyllosoma stages.

The scarcity of the larvae in general may, however, indicate in part a tendency of the larvae to seek levels so near the bottom that they are not adequately sampled by most of our plankton towing. That this may be so, at least in shallow water, is suggested by the finding of twenty specimens in a dredge haul made by Robert Bieri and John Bradshaw of Scripps Institution with a small specially constructed net dragged along the bottom for a distance of 17 meters at a depth of 13 meters. These larvae were, however, all in stage I and may have been just recently released in the area and not yet undergone dispersal by swimming or water currents. Midwater-trawl hauls of long duration taken at depths ranging to 1500 meters or more over very deep water have yielded later stage larvae. The depth of actual catch, however, is not known and the amount of water screened in these hauls is relatively enormous when compared with that screened during the 1-meter net hauls. In view of the many deep hauls that have not yielded larvae, no conclusions can be made from these instances relative to the depth of concentration or habit of seeking the bottom.

Nakamura (1940) working with the Japanese species, *Panulirus japonicus,* states that the embryonic period is passed through in about one month and he deduced from related data that the phyllosoma stages require about the same length of time to reach the puerulus stage. This seems much too short a period.

The status of the systematics of phyllosoma larvae was reviewed by Gurney (1936) in his analysis of the *Discovery* collection which in some 400 specimens contained about a dozen different generic or specific forms. Owing to lack of complete series, however, characters used for recognition of several genera, including *Panulirus,* were given with considerable reservation. The present complete series of larvae of *Panulirus interruptus* is therefore of special use toward establishing the characters which delineate that genus.

The larval structure of *Panulirus interruptus* agrees in general with that of larvae known or believed to belong to other species of the genus. There is, however, a notable difference, no doubt specific, in the relative widths of the main divisions of the body of the older larvae.

On the basis of material available to him, Gurney (1936) concluded

provisionally that in the genus *Panulirus* the hind-body is wider, sometimes much wider, than the fore-body. This diagnostic characteristic was established for later stages on Gurney's *Panulirus* larvae A, B *(P. argus),* and D. Later Lebour (1950) and Lewis (1951), dealing with *Panulirus argus,* verify that the hind-body of that species becomes noticeably broader in the later stages. In *Panulirus interruptus,* however, the character does not hold, for in this species the hind-body has attained the width of the fore-body in stage III and remains equal in width throughout the ensuing stages. Thus the diagnostic description must be amended to accommodate not only the young stages of *Panulirus argus* as pointed out by Lebour (1950) but also the later stages of the present species. This makes it a rather unreliable generic characteristic, but useful specifically.

Just what larval details must be stressed in the diagnosis of the species of *Panulirus* are, of course, not fully established as yet and it is likely that useful characters have been overlooked or omitted in the descriptions of series or isolated stages of larvae. Among the characters that may have some specific use are the spines observed in *Panulirus interruptus* on the ventral side of the thorax at the base of each leg. Such spines are not shown or mentioned for other species, but Lewis (1951) in figure 4 B. and C. does show a series of structures suggesting low knobs on the ventral mid-line of the thorax in later stages of *Panulirus argus.* The presence and degree of persistence of coxal spines on the legs and third maxilliped appear also to vary with species within the same genus. In *Panulirus argus* no coxal spine develops on the third maxilliped and those on the legs persist only through the fifth stage, whereas in *Panulirus interruptus* the third maxilliped and all but the fourth and fifth pairs of legs bear these spines up through the ninth stage. There may be some variability in the later stages. The presence of a spine at the distal end of the basipod adjacent to the exopod of the first three pairs of legs as mentioned in the text for *P. gracilis* serves to separate that species from *P. interruptus,* but other characters such as relatively wider fore-body may be needed to separate it from Gurney's phyllosoma *Panulirus* A.

An obvious difficulty in establishing certainty in the systematics of phyllosoma larvae arises either from a considerable variability in the larval structures of some species or from erroneous descriptions as shown by the following unexplained discrepancies. Kinoshita (1934) states that in stage I *Panulirus japonicus* has no exopod on the third maxilliped and yet Nakazawa (1917) in figure I shows the exopod to be present in this stage. Crawford and De Smidt (1922) in figure 273 show no exopod on this appendage in stage I of *Panulirus argus* yet subsequent workers agree that the exopod is present.

SUMMARY

The spiny lobster, *Panulirus interruptus* (Randall), passes through eleven rather poorly defined phyllosoma larval stages. The larvae are planktonic during these stages which require several months for completion.

Through metamorphosis, the last phyllosoma stage becomes the puerulus stage which resembles the adult and becomes benthonic.

All of the phyllosoma stages and the puerulus stage are described and figured.

A second species of phyllosoma referred to *Panulirus gracilis* Streets was found overlapping the range of *P. interruptus* off Baja California, and in the Gulf of California. A description is given of this larva enabling its separation from *P. interruptus*.

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